

**Two New Species of Porostome Nudibranchs (Family Dendrodorididae) from the Coasts of California (USA) and Baja California (Mexico)**

**Sandra V. Millen<sup>1</sup> and Hans Bertsch<sup>2,3</sup>**

<sup>1</sup> Department of Zoology, University of British Columbia, 6270 University Blvd., Vancouver, B.C., Canada, V6T 1Z4; Email: millen@zoology.ubc.ca; <sup>2</sup> 192 Imperial Beach Blvd., #A, Imperial Beach, CA 91932, USA; Email: hansmarvida@sbcglobal.net.

**A new species of porostome nudibranch, *Dendrodoris stohleri*, with a yellow to cream body color and irregular black spots, is described from the northern Gulf of California, Mexico. Its discrete and intense spotting, which does not appear on the sole of the foot, is distinctive. A second species, *Dendrodoris behrensi*, is described from specimens collected from southern California and the Pacific side of the northern Baja California peninsula, Mexico. It is white with a smooth, elongate body and large brown irregularly distributed spots and pale rhinophores and gills.**

KEY WORDS: Opisthobranchia, Porostomata, *Dendrodoris*, new nudibranch species.

A number of recent papers have enlarged our knowledge of the anatomical (Valdés et al. 1996; Brodie et al. 1997) and histological (Wägele et al. 1999; Brodie 2001) aspects of the Family Dendrodorididae. Despite these studies, there remains a dichotomy in the terms assigned to the anatomical parts of these animals. In this paper, we have followed recent terminology with the more traditional terms given in brackets. Investigations have also been made to clarify either by molecular (Thollessen 2000; Wollscheid-Lengeling et al. 2001; Valdés 2003) or cladistic means (Valdés and Gosliner 1999; Valdés 2002) the position of the family in relation to other nudibranchs. It is currently believed that the family Dendrodorididae is nested within the cryptobranch dorids (Valdés and Gosliner 1999; Wollscheid-Lengeling et al. 2001; Valdés 2002, 2003) and there is support for the monophyly of the Porostomata with the radula-less dorids Dendrodorididae and Phyllidiidae forming sister clades (Valdés and Gosliner 1999; Thollessen 2000; Valdés 2002, 2003).

In the family Dendrodorididae, nudibranchs lack a radula and are often variable in color, which makes them difficult to identify. There are seven species in two genera, *Doriopsilla* and *Dendrodoris* that are currently recognized as occurring along the Pacific coast of North America. At one time, the two genera were merged (Steinberg 1961), but they are now separated by a large number of morphological features, some recognized earlier (Eliot 1906; Pruvot-Fol 1930, 1954) and others more recently (see Valdés and Gosliner 1999; Gosliner et al. 1999; Brodie 2001). The genus *Doriopsilla* is characterized by having synapomorphies of an eccentric anus (to the left), a flat, non-tubular prostate gland, and buccal ganglia that are dorsal to the esophagus but close to the central nerve ring. Like many cryptobranch dorid nudibranchs, they usually have small rounded tubercles and spicules on the notum, one duct to their bursa copulatrix and eversible spines on the penis. Five

<sup>3</sup> Research Associate, California Academy of Sciences.

species along the Pacific coast of North America belong to this genus, *Doriopsilla albopunctata* (Cooper, 1863), *D. gemela* Gosliner et al., 1999, *D. janaina* Marcus and Marcus, 1967, *D. nigromaculata* (Cockerell in Cockerell and Eliot, 1905) (= *D. rowena* Marcus and Marcus, 1967, according to Valdés and Behrens 1998; Valdés and Ortea 1998) and *D. spaldingi* Valdés and Behrens, 1998. It has been postulated that *D. janaina* is possibly a junior synonym of *D. areolata* Bergh, 1880 (see Valdés and Ortea 1997) although Valdés and Gosliner (1999) retain them separately.

The genus *Dendrodoris* is characterized by synapomorphies of a soft body, lacking spicules even when tubercles are present, and a posterior mouth, located within a deep notch of the foot. Internally, there are paired ptyaline (oral) glands with a muscular duct and small esophageal glands. The central nervous system usually has ganglionic tubercles, and the buccal ganglia are far posterior on the esophagus, just in front of the esophageal (salivary) glands. The reproductive system usually has two ducts to the bursa copulatrix and the spines on the vas deferens usually have long bases (see Valdés and Gosliner 1999). There is a common but problematic species in this genus, commonly known as *Dendrodoris krebsii* (Mörch, 1863), found along the Pacific coast from the Gulf of California to Panama and the Galapagos that has recently been assigned to the Indo-Pacific species *D. fumata* Rüppell and Leuckart, 1930 (Behrens 2004). However, a reassessment of *D. fumata* suggests that the black color variety with a red rim is in fact a separate species, *Dendrodoris arborescens* (Collingwood, 1881) based on differing larval forms (Brodie and Calado, in press). Since on the Pacific coast, specimens from the outer coast of Baja California and the Gulf of California are black with a red rim, and specimens further south, in Jalisco, Mexico and the Galapagos are variable from grey to red, further investigation must be made before settling upon a name for the Pacific northeast species. Recently described by Behrens and Valdés (2004) is a deep-water California species, *D. azineae*, which has a white body and dark purple-tipped gills and rhinophores. Two undescribed species belonging to the genus *Dendrodoris* are described in this paper, one with a yellow or cream body and small black spots, from the Gulf of California, and the other with a white body and large brown blotches from the Pacific coast of southern California and Baja California.

**Subclass Opisthobranchia**  
**Order Nudibranchia**  
**Porostomata Bergh, 1891**  
**Family Dendrodorididae O'Donoghue, 1924**

**Genus *Dendrodoris* Ehrenberg, 1831**

TYPE SPECIES: *Dendrodoris lugubris* Ehrenberg, 1831 [by subsequent designation by Gray, 1847].

***Dendrodoris stohleri* Millen and Bertsch, sp. nov.**

Figs. 1A–B, 2A, 3, 4 A–C.

*Dendrodoris* sp. Bertsch 1991:18.

**ETYMOLOGY.**— This species is named in honor of our colleague, mentor and friend, Dr. Rudolf Stohler (1901–2000), for his numerous contributions to malacology. As founding editor of *The Veliger*, he supported and encouraged many young students (Bertsch 2000). We remember his eccentricities and his graciousness — a true gentleman and scholar!

**MATERIAL EXAMINED.**— HOLOTYPE: CASIZ 166884, 10 mm, preserved length, 2–3 m. depth, Herradura, Bahía de los Ángeles, Baja California, Mexico, 18 February 1999, S. Millen. PARATYPES: eight specimens, CASIZ 166887, intertidal, Isla Coronado, 27 April 1986, H. Bertsch, 1 dissected. Two specimens, CASIZ 069301, Punta la Gringa, Bahía de los Ángeles, 27 April 1986, H. Bertsch, one dissected. Four spec-

imens, CASIZ 073507, Puerto Don Juan, Bahía de los Ángeles, Baja California, Mexico, 5 October 1984, Gosliner, Bertsch and Ferreira. Two specimens, CASIZ 73505, 10–12 meters, Isla Coronado, Bahía de los Ángeles, Baja California, Mexico, 4 October 1984, R. Van Syoc and D. Mulliner. Three specimens, CASIZ 166885, 2–3 m. depth, Herradura, Bahía de los Ángeles, Mexico, 18 February 1999, S. Millen. One specimen, CASIZ 166886, 8 m., Cuevitas, Bahía de los Ángeles, Mexico, 19 February 1999, S. Millen, dissected.

**EXTERNAL MORPHOLOGY.**— This species has a low, elongate-oval body with a moderately sized, slightly crenulate margin (Figs. 1 A–B). The maximum size of a preserved animal measured 24 mm with a mantle margin 3 mm wide. The notum is smooth. There are a few fine striations in the mantle margin, approximately 3 per mm, dividing towards the edge. The straight rhinophores have 8–10 lamellae sloping posteriorly from an anterior ridge, to meet posteriorly in a V. The tip is elevated and flattened. The rhinophore opening is raised slightly and smooth. The low branchial pocket is smooth. There are 6–7 posteriorly directed tripinnate gills. Ventrally the foot is bilabiate as far posterior as the gonopore with both the labium and foot notched in the centre where the pore-like mouth opening is located. There are two small, triangular, unnotched tentacles fused to the upper labium of the foot. The foot has a small flange and a bluntly rounded posterior, which trails slightly when the animal is crawling.

The ground color is pale cream to dark golden yellow. Small irregular black spots are scattered on the dorsum but rarely on the mantle margin. The rhinophores are slightly darker than the ground color and may have a few black spots. The gills are the same as the ground color and may also have a few spots. The ventral surface is the same as the ground color. A few animals had one or two spots on the sides, but never on the foot or the underside of the mantle.

**ANATOMY.**— The notum is thick and soft with many lacunae just above the basal layer. It is strengthened by vertical connective tissue strands, but has no spicules. The viscera are within a colorless envelope. The digestive tract is illustrated in Figure 2 A. The buccal bulb (oral tube) is mus-

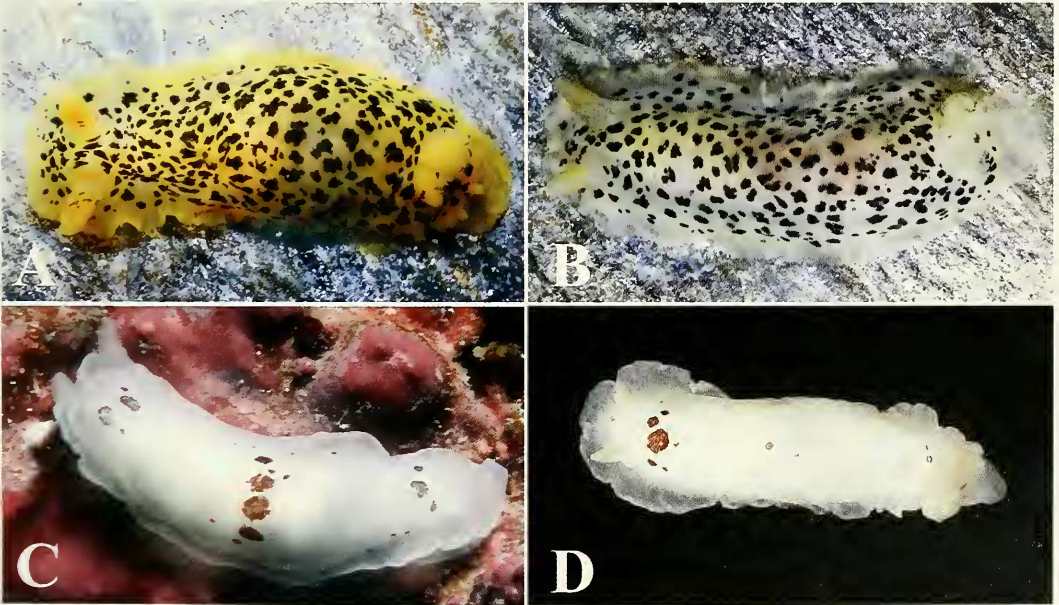


FIGURE 1. *Dendrodoris stohleri* sp. nov. (166885). A. Dark color form. B. Light color form. Both photos by Mike Miller. Specimens from Bahía de los Ángeles, Mexico, Feb. 1999. C. *Dendrodoris behrensi* sp. nov. (082088). Photo by Mark Chamberlain, specimen from San Clemente Is., California, USA, Feb., 1988. D. *Dendrodoris behrensi* sp. nov. (070838). Photo by Gary McDonald. Specimen from Malibu, California, USA, Oct. 1971.

cular, short and wide. Posteriorly it is attached to the body wall by lateral muscle bundles, three on each side. Ventrally, the long duct from the bilobed ptyaline (oral) glands enters the buccal bulb at its junction with the pharynx. The ptyaline duct widens and branches into two before it enters each irregularly rounded, somewhat flattened, light colored gland. The narrow, tubular, pharynx is highly muscular. It passes through the nerve ring and bends, to the left and right in a reverse S-shape in contracted specimens, in a C-shape in relaxed specimens. It constricts at its junction with the esophagus. Just anterior to this junction, on the dorsal surface, lie two round buccal ganglia. Posterior to this junction, the esophagus has two lateral, oval, esophageal (salivary) glands. Next to each gland are two slender retractor muscles that run half way to the first bend of the esophagus and insert on the esophagus. At this point, the esophagus widens to at least twice the diameter of the pharynx, becomes glandular and is capable of distending when filled with food. In its distended state, it is smooth. When contracted its surface is somewhat irregular. The esophagus bends in an inverted S-shape to the left, then right, back to the midline. The esophagus is over twice as long as the pharynx (2.4:1). Posteriorly there is an internal, muscular sphincter controlling food flow into a thinner walled stomach, which can be tubular and the same diameter as the esophagus or expanded like a balloon when full of food. The remainder of the stomach is embedded in the confluent digestive glands. The intestine emerges near the centre of the digestive glands and turns sharply to the right. There is a small, round, anterior pyloric gland (caecum). The intestine lies over the digestive glands and under the renal-pericardial complex. It narrows to the anus emptying on a small, smooth, medial papilla, which is posteriorly placed in the gill circlelet.

The heart (Fig. 2A) forms a broad triangular auricle with a large anterior ventricle. A prominent renal syrinx, on the posterior right side, drains the pericardial sac. A medial aorta runs anteriorly from the ventricle to the region of the central nervous system. Anterior to the digestive gland, to the left of the aorta, is a moderately large, flat, irregular blood gland, which lies within the bend of the esophagus and posterior to the central nervous system.

The central nervous system (Fig. 2A) has fused cerebro-pleural ganglia. These ganglia are separated from each other by a very slight mid-line depression. They have large nerve cells, which nevertheless form a smooth, non-tuberculate surface. The stout rhinophoral nerves each have a slightly larger gan-

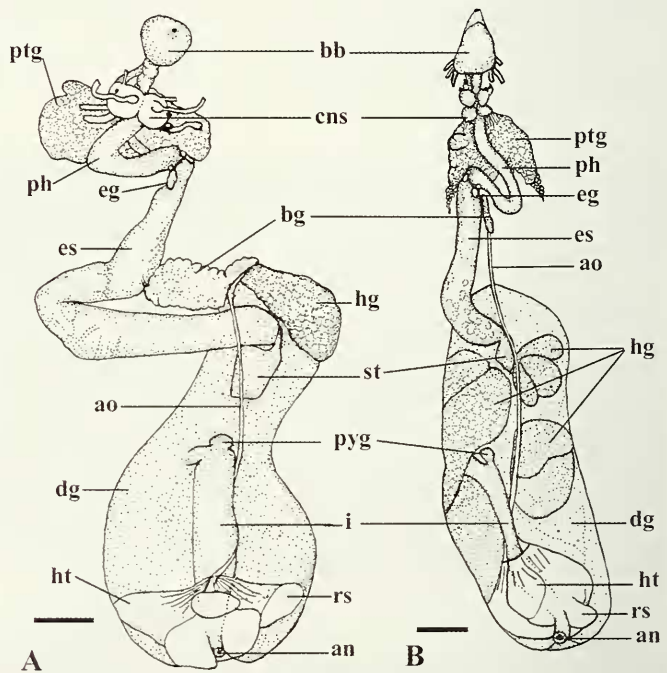


FIGURE 2. *Dendrodoris stohleri* sp. nov. (166886). A. Digestive tract drawn by camera lucida. Scale bar = 1 mm. B. *Dendrodoris behrensi* sp. nov. (171659). Digestive tract drawn by camera lucida. Scale bar = 1 mm. Key: ao=aorta, an=anus, bb=buccal bulb, bg=blood gland, CNS = central nervous system, dg=digestive gland, eg=esophageal gland, es=esophagus, hg=hermaproditic gland, ht=heart, i=intestine, ph=pharynx, ptg=ptyaline gland, pyg=pyloric gland, rs=renal sac, st=stomach.

gion at their bases. The eyes are large, almost sessile, with clear lenses. The small otocysts with otoconia are located just posterior and ventral to the eyes. The cerebro-buccal connectives are long and separate, the round buccal ganglia lie dorso-laterally on the posterior portion of the pharynx. There is a narrow, posterior, visceral commissure. The smaller, round pedal ganglia are ventral to the cerebral part of the cerebro-pleurals and the pharynx. They are connected by a short, broader, posterior, parapedal commissure.

The large hermaphroditic gland (ovotestis) is separate from the digestive glands and anterior to them. The reproductive system (Fig. 3) has a long pre-ampullary duct that widens into a tubular ampulla with one loop. The short post-ampulla duct bifurcates into a long oviduct and the prostatic portion of the vas deferens. The prostate is wide and long. It loops back on itself, completely enveloping the bursa copulatrix, narrows and continues as a highly convoluted tubular duct. The narrower muscular deferent (ejaculatory) duct of the vas deferens is coiled distally, widening at the penial sac before it terminates in the common genital atrium. The penis is armed with many rows of large, almost straight chitinous spines from 18–28  $\mu\text{m}$  in height with small bases (Figs. 4A–C). There are up to 22 spines in each row. The common atrium is elongate and plicate internally. The long, tubular vaginal duct is internally villous and wider distally. It narrows gradually and convolutes slightly before opening into the large, rounded bursa copulatrix. A separate, long, narrow uterine duct connects the bursa copulatrix to the female gland mass close to the entrance of the oviduct. A short, wide duct from the small, oval seminal receptacle joins the uterine duct near its entrance to the gland mass. The bursa copulatrix is approximately 4.5 times larger than the seminal receptacle. The female gland mass consists of an anterior, granular, yellow portion dorsal to the entrances of the oviduct and uterine ducts and a highly convoluted, firm, white mucus gland with a slightly differentiated lobe at the proximal end of the long nidamental duct. The nidamental duct adheres closely to the atrium and opens posterior to it. There is no vestibular gland. A protruding flap separates the genital openings. They are located high on the right side of the animal, one quarter of the way back from the anterior mantle margin.

**NATURAL HISTORY.**— The known range of *Dendrodoris stohleri* is within Bahía de los Ángeles (29°0'N, 113°30'W), in the Gulf of California, Mexico. It is restricted to the islands and outer shore locations. This species occurs extremely rarely at the frequently sampled and readily accessible shore sites (within 10 km of the town of Bahía de los Ángeles) Cuevitas and Punta la Gringa. During the 10-year period from 1992–2001, one of us (HB) regularly surveyed the opisthobranch fauna of these sites. Of 6,095 specimens observed, only 1 was *D. stohleri*. However, over 30 spec-

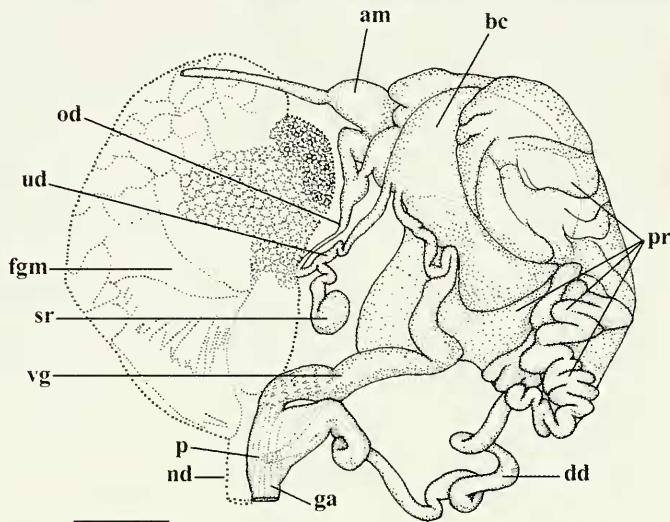


FIGURE 3. *Dendrodoris stohleri* sp. nov. (166887). Reproductive system drawn by camera lucida. Scale bar = 1 mm. Key: am=ampulla, bc=bursa copulatrix, dd=deferent duct, fgm=female gland mass, ga=genital atrium, nd=nidamental duct, od=oviduct, p=penis, pr=prostate, ud=uterine duct, vg=vagina.

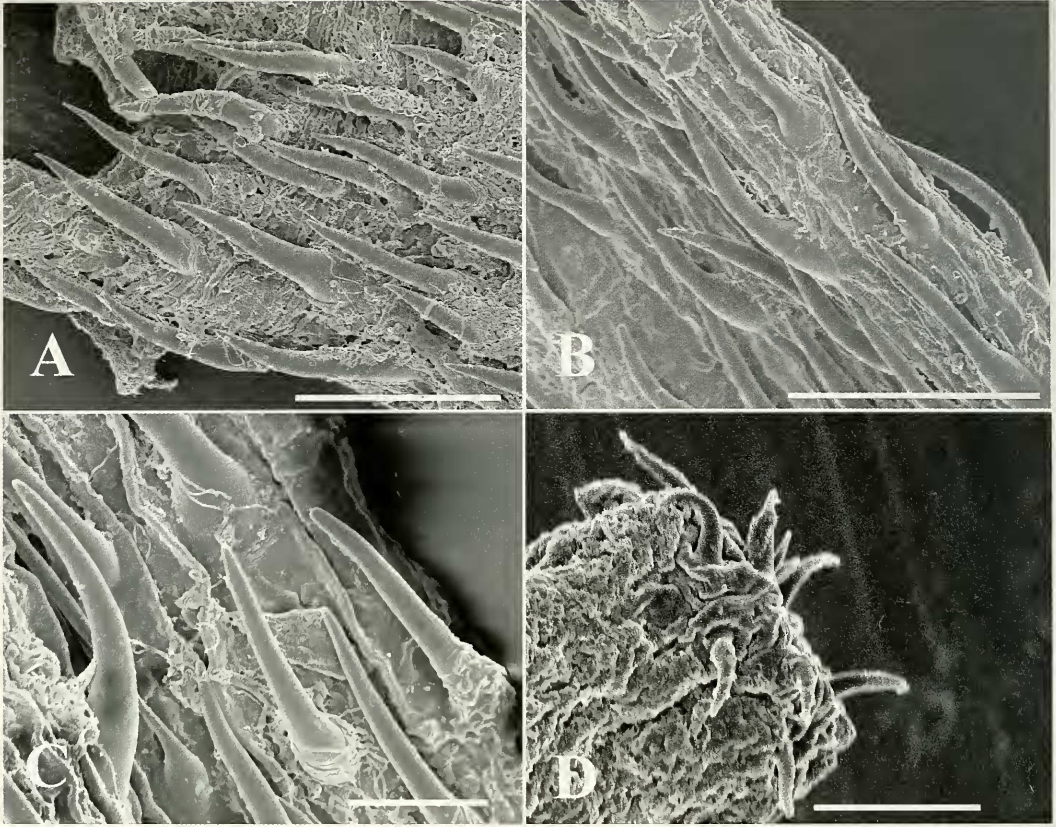


FIGURE 4. *Dendrodoris stohleri* sp. nov. 166887). A. Penial spines from distal end of penis of Scale bar = 30  $\mu$ m. B. Penial spines from middle of penis. Scale bar = 30  $\mu$ m. C. Penial spines from proximal end of penis Scale bar = 30  $\mu$ m. D. *D. behrensi* sp. nov. (171658). Penial spines from distal end of penis. Scale bar = 10  $\mu$ m.

imens have been observed by HB at the islands and reefs between Puerto Don Juan, Isla Calabeza, Isla Coronado, and at the intertidal zone of the "old turtle farm" at Isla Coronado.

This distributional pattern within Bahía de los Ángeles clearly illustrates the 2 major opisthobranch communities within this bay as reported by Bertsch et al. 1998 (see their Fig. 1, map showing the different regions).

This species has been found in February, April, October and November, with mature animals in April. They are found intertidally and subtidally under rocks, to a depth of 12 m. *Dendrodoris stohleri* appears to feed on an encrusting yellow demosponge.

**DISCUSSION.**— *Dendrodoris stohleri* can be distinguished from all others in the genus by its smooth body with distinct black spots, not blotches, on a yellow or cream background, light gills and rhinophores and no dark spots on the foot. *Dendrodoris sadoensis* Baba, 1993 is dull yellow with larger black blotches and black spots are also found on the underside. Internal differences are that the penis is unarmed, the bursae are close to each other in size, the proximal prostate is not enlarged and the vagina is threadlike.

The reproductive system of *D. stohleri* lacks a vestibular gland and has a wide, massive prostate followed by a convoluted narrower prostatic section, then a shorter, muscular region. The bursa copulatrix is unusually large compared to the seminal receptacle. In these respects *D. stoh-*

*leri* is similar to *D. tuberculosa* Quoy and Gaimard, 1832 and *D. limbata* (Cuvier, 1804). It can be clearly distinguished externally from *D. tuberculosa* by its smaller size, higher oval shape, smooth dorsum and yellow or cream ground color. Internal differences are that *D. tuberculosa* has irregular oral glands, an interdigitated hermaphroditic gland, no distal post-ampullar duct, a more tubular prostate and longer bases on the penial hooks.

Light colored tentacles and rhinophores and smaller spots, never ventral, distinguish *D. stohleri* externally from the yellow and spotted variety of *D. limbata*, which is usually dark brown with a yellow rim, although internally they are similar. A cladistic analysis, which includes 9 species in the genus *Dendrodoris* separates these 9 species by 13 characters (Valdés and Gosliner 1999). Using the *Dendrodoris* portion of this tree, rooted on *D. coronata*, results in the same topography as presented in Figure 23 in Valdés and Gosliner (1999:353). The addition of *D. stohleri* indicates it is a sister species to *D. limbata*. When an allzero ancestor is used as the outgroup, the topography changes slightly. *Dendrodoris coronata* remains basal and *D. limbata* once more pairs with *D. stohleri* followed by *D. grandiflora* and *D. fumata* which are basal to the remaining species. In common, *D. stohleri* and *D. limbata* have a flattened proximal portion of the prostate and penial spines, which have short bases. A distal post-ampullary duct, present in *D. stohleri*, is absent in *D. limbata*.

***Dendrodoris behrensi* Millen and Bertsch, sp. nov.**

Figs. 1C–D, 2B, 4D, 5.

*Dendrodoris* sp. Lee and Brophy, 1969:220; Behrens, 1980:101, fig. 141.

*Dendrodoris* species b: McDonald and Nybakken, 1981:54–55, fig. 58; McDonald, 1983:171.

*Dendrodoris* sp. 3: Behrens, 1991:72, fig. 132.

*Dendrodoris* sp. 4: Rudman, 2003. Sea Slug Forum fact sheet.

**ETYMOLOGY.**— This species is named for our friend and colleague David W. Behrens, whose books, articles and photographs have significantly contributed to our knowledge of opisthobranchs.

**MATERIAL EXAMINED.**— HOLOTYPE: 16 mm. preserved length, CASIZ 069303, Pyramid Point, San Clemente Is., intertidal, 14 Feb 1988, R. Van Syoc. PARATYPES: one specimen, CASIZ 071367, Castle Rock, San Miguel Island, 25–40 ft., 24 October 1986, R. Van Syoc. Two specimens, CASIZ 171658, Pyramid Point, San Clemente Is., intertidal, 14 February 1988, R. Van Syoc, one partially dissected. One specimen, CASIZ 068309, Pt. Pinos, Pacific Grove, July 1932, G.E. MacGinitie, MacFarland collection. One specimen, dissected, CASIZ 69299, Abalone cove, Palos Verdes, under rock, 15 ft., 29 July 1982, P.A. Haaker. One specimen, CASIZ 069300, Jim Gatewood, California, no locality. One specimen, CASIZ 070838, Dume Rocks, Pt. Dume, Malibu, 9 Oct 1971, S. Anderson, McDonald collection. One specimen, CASIZ 071019, Santa Monica Bay, 25 fathoms, 7 July 1971, S. Anderson, McDonald collection. One specimen, CASIZ 082088, n. end of West cove, San Clemente Is., intertidal, 17 February 1988, R. Van Syoc. One specimen, CASIZ 068310, Pacific Grove, large tide pool, 27 July 1929, F.M. MacFarland. One specimen, CASIZ 070836, dissected, 10 feet. California, no locality, S. Anderson, 20 October 1971, McDonald collection. One specimen, CASIZ 072006, ½ m s.w. of Pescadero Pt., the Pinnacles, Monterey county, 17 October 1975, Mark Silberstein, McDonald collection. One specimen, CASIZ 068311, Pacific Grove, Point Pinos, large tide pool, 21 July 1921, F.M. MacFarland. Three specimens, CASIZ 171659, 1 dissected, Cabo Falsa, Bahía de San Quintín, Baja California, Mexico, 22 May 2001, Jeff Goddard. One specimen, CASIZ 171660, dissected, Cabo Falsa, Bahía de San Quintín, Baja California, Mexico, 27 May 2001, Jeff Goddard.

**EXTERNAL MORPHOLOGY.**— The body is slender and elongate with a narrow mantle margin, which undulates slightly (Figure 1C–D). The total length is up to 20 mm. The dorsum is smooth and without tubercles or spicules. There are some radiating connective tissue strands in the mantle margin. The rhinophores are straight, with 7–13 long sloping lamellae. The rhinophoral and branchial sheaths are slightly raised and smooth. There are 3–6 bipinnate or weakly tripinnate gills

arranged in a circlet broken by the mid-posterior anus. The ground color is semi-translucent white or pale cream. There are round dark reddish brown or chocolate brown spots on the notum but not the mantle rim. These vary in size, but the larger spots tend to be clustered in four areas in the mid-line. These are, in front of the rhinophores, behind the rhinophores, the middle of the body and in front of the gills. Sometimes the anterior-most cluster is absent. Smaller spots are scattered towards the edges of the dorsum. Rhinophores and gills are white or cream; the gills may have a very few, small, brown spots near the tips. The ventral surface of the foot has no spots, but small spots may be present on the sides of the body and the dorsal surface of the trailing posterior foot. The head is small, with a pore-like mouth opening located within the notch of the foot. The short, ungrooved tentacles are attached to the foot and body wall. The foot is bilabiate with only the upper labium notched in the centre line; the main portion of the foot is entire, deeply wrinkled near the mouth. The double edge continues to the region of the reproductive openings. The foot flange is small and undulating. The posterior end is widely rounded.

**ANATOMY.**— The notum is soft, without spicules and with fine connective tissue strands. The basal layer is thick and just above it is a layer with small lacunae. The viscera are within a colorless envelope. The digestive tract is illustrated in Figure 2B. The buccal bulb (oral tube) is conical and muscular. Posteriorly it is attached to the body wall by three slender muscles on each side. Ventrally, a long duct from the bilobed ptyaline (oral) glands enters the buccal bulb at its junction with the pharynx. This ptyaline duct branches into two within each gland, which are close together anteriorly. In a juvenile specimen, both glands were clearly separate. Posteriorly, each gland has a triangular white patch of larger round cells. The narrow, tubular, gradually widening pharynx is highly muscular. It bends in a reverse S-shape and sometimes loops before it passes through the nerve ring. Posterior to the nerve ring, the pharynx bends in a reverse C- or S-shape and constricts at its junction with the esophagus. Just anterior to this junction lie the two round, dorsal buccal ganglia. Posterior to the junction are two small, round, lateral esophageal (salivary) glands. Next to each gland are two slender retractor muscles, which lie on either side of the anterior portion of the esophagus. After their insertion on the esophagus, the esophagus gradually widens, curves, and becomes irregular in texture. The esophagus is longer than the pharynx (1.4:1). Posteriorly, a sphincter separates the esophagus from the short, exposed section of the stomach. The remainder of the stomach is embedded in the confluent digestive glands. The intestine emerges from the digestive glands left of the midline and bends to the right. There is a short stalked, round, anterior pyloric gland (caecum). The narrow intestine curves medially to run posteriorly down the midline where it exits on the smooth anal papilla, located posteriorly in the gill circlet.

The heart (Fig. 2B) forms a broad triangular auricle with a large, rounded anterior ventricle. A prominent renal syrx, on the posterior right side, drains the pericardial sac. A medial aorta runs anteriorly from the ventricle to the region of the central nervous system. A small white blood gland is located to the right of the esophagus, with ducts attached to the esophagus at its bend.

In the central nervous system (Fig. 2B), the elongate cerebro-pleural ganglia are fused but can be distinguished by a furrow separating the anterior cerebral ganglia from the posterior pleural ganglia. There is a distinct mid-line furrow separating the two cerebro-pleural ganglia. The dorsal surface is smooth although large cells can be seen. The stout rhinophoral nerves each have a large ganglion at their bases. The eyes are moderate in size and almost sessile. The cerebro-buccal connectives are long and thin, within the same connective tissue, extending to two round buccal ganglia, side by side on the dorsal posterior portion of the pharynx. The large, round pedal ganglia are ventral to the cerebro-pleural ganglia and the pharynx. They are connected by a very short commissure and have smaller nerve cells.

The hermaphroditic gland (ovotestis) is spread over the digestive glands. The white female fol-



licles form clusters with granular, creamy-yellow male follicles between the clusters. The reproductive system (Fig. 5) has a long pre-ampullary duct, which widens abruptly into a bean-shaped ampulla. The ampulla has a distinct post ampullary duct, which bifurcates into a long oviduct and a vas deferens. The prostatic portion of the vas deferens is tubular and not greatly enlarged. The narrow, muscular deferent (ejaculatory) duct of the vas deferens is shorter than the prostatic portion. It widens slightly for half of its length and then enters the common atrium with a short conical penis. The penis tip is armed with 17–18 rows, 5–6 per row, of small, recurved spines 5.4–7.5  $\mu\text{m}$  in height (Fig. 4D). The remainder of the vas deferens appears to have no spines. The elongate genital atrium is glandular, striated and papillate internally. Between the male and female ducts is a muscular section with attached muscle strands from the junction of the prostatic and ejaculatory portion of the vas deferens. Other strands run to the seminal receptacle. The long, tubular vaginal duct is threadlike and muscular throughout its length. It enters a round or oval bursa copulatrix. The uterine duct is distinct but is attached to the vagina for a short distance, then it separates and convolutes. The oval seminal receptacle has a moderately long duct, which joins the uterine duct near its junction with the oviduct. The oviduct and uterine duct together enter the female gland mass. The bursa copulatrix varies from equal in size to the seminal receptacle to twice its size. The female gland mass is large, elongate, and oval in shape. It consists of a large, granular pinkish or cream-colored section into which the combined uterine and oviduct enters ventrally and a highly convoluted, firm, white mucus gland. There is a soft area at the base of the long nidamental duct. There is no vestibular gland. The nidamental duct adheres to the atrium and opens posterior to it. The reproductive openings usually appear as one small, round depression located high on the right side approximately one third of the way back from the anterior mantle margin, but the genital atrium can form an expanded papilla with the female gland mass opening posteriorly at its base.

The reproductive system (Fig. 5) has a long pre-ampullary duct, which widens abruptly into a bean-shaped ampulla. The ampulla has a distinct post ampullary duct, which bifurcates into a long oviduct and a vas deferens. The prostatic portion of the vas deferens is tubular and not greatly enlarged. The narrow, muscular deferent (ejaculatory) duct of the vas deferens is shorter than the prostatic portion. It widens slightly for half of its length and then enters the common atrium with a short conical penis. The penis tip is armed with 17–18 rows, 5–6 per row, of small, recurved spines 5.4–7.5  $\mu\text{m}$  in height (Fig. 4D). The remainder of the vas deferens appears to have no spines. The elongate genital atrium is glandular, striated and papillate internally. Between the male and female ducts is a muscular section with attached muscle strands from the junction of the prostatic and ejaculatory portion of the vas deferens. Other strands run to the seminal receptacle. The long, tubular vaginal duct is threadlike and muscular throughout its length. It enters a round or oval bursa copulatrix. The uterine duct is distinct but is attached to the vagina for a short distance, then it separates and convolutes. The oval seminal receptacle has a moderately long duct, which joins the uterine duct near its junction with the oviduct. The oviduct and uterine duct together enter the female gland mass. The bursa copulatrix varies from equal in size to the seminal receptacle to twice its size. The female gland mass is large, elongate, and oval in shape. It consists of a large, granular pinkish or cream-colored section into which the combined uterine and oviduct enters ventrally and a highly convoluted, firm, white mucus gland. There is a soft area at the base of the long nidamental duct. There is no vestibular gland. The nidamental duct adheres to the atrium and opens posterior to it. The reproductive openings usually appear as one small, round depression located high on the right side approximately one third of the way back from the anterior mantle margin, but the genital atrium can form an expanded papilla with the female gland mass opening posteriorly at its base.

**NATURAL HISTORY.**— This species was first collected from the Great Tide Pool, in Pacific Grove, California, in 1921 and again in 1929 by Frank Mace MacFarland. The known range of *Dendrodoris behrensi* is from Point Pinos, Monterey Bay, California (approximately 37°27'N; 121°55'W), to the San Benitos Islands, Baja California, Mexico (approximately 28°18'N; 115°34'W). This species has been found in February, May, July and October, intertidally and subtidally to a depth of 50 m. The prey sponge of this species is unknown. The spawn and larval development have been studied by Goddard (2005a, b) and it is known to have ametamorphic direct development.

**DISCUSSION.**— The smooth dorsum, clustered, irregular chocolate brown spots on an off-white

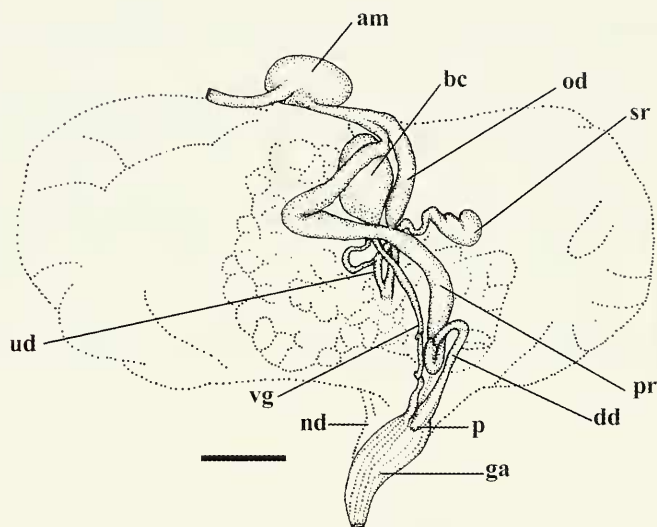


FIGURE 5. *Dendrodoris behrensi* sp. nov. (070836). Reproductive system drawn by camera lucida. Scale bar= 1 mm. Key: am=ampulla, bc=bursa copulatrix, dd=deferent duct, fgm=female gland mass, ga=genital atrium, nd=nidamental duct, od=oviduct, p=penis, pr=prostate, ud=uterine duct, vg=vagina.

background and pale rhinophores and gills found in this species are distinctive. Other species with similar coloration are *D. albobrunnea* Allan, 1933 and *D. elongata* Baba, 1936. Both of these species can be distinguished by their flatter, more elongate bodies, presence of small tubercles, regular brown spotting and leach-like locomotion. Internally, *D. elongata* is not known, but *D. albobrunnea* has more rows of penial spines, which have long bases and a vestibular gland is present. *Dendrodoris coronata* Kay and Young, 1969 can be distinguished by small scattered pustules and a transverse raised ridge located anterior to the gills, which has large crown-like pustules. Internally it has no penial hooks. When *D. behrensi* is added to the cladograms along with *D. stohleri*, it lies just basal to the sibling species *D. limbata* and *D. stohleri*. It differs in that it has a smaller, tubular prostate and fewer rows of penial hooks but the hooks of all three species have short bases. A recently described, smooth, white species from California, *D. azinae* Behrens and Valdés, 2004 can be distinguished by its dark purple-tipped gills and rhinophores and lack of brown spots on the body.

#### ACKNOWLEDGMENTS

We thank those who helped us collect, or gave us specimens or photos, enabling us to understand the zoogeography and anatomy of these two new species. Assistance with *Dendrodoris stohleri* is gratefully acknowledged to Brian Coleman, Carolina Espinoza, Antonio Ferreira, Terrence Gosliner, Alan Grant, Michael D. Miller, David K. Mulliner, Antonio Resendiz, Tom Smith, and Robert van Syoc. For *Dendrodoris behrensi* we thank Shane Anderson, Mark Chamberlain, Jeff Goddard, P.A. Haaker, Frank Mace MacFarland, George E. MacGinitie, Gary McDonald, and Mark Silberstein.

This research was partly funded by the Department of Zoology, University of British Columbia, to Sandra Millen.

We especially thank the graciousness and inspiration of Rudolf Stohler and David Behrens, without whom this manuscript would not have been possible.

#### REFERENCES

- BEHRENS, D.W. 1980. *Pacific Coast Nudibranchs, A Guide to the Opisthobranchs of the Northeastern Pacific*. Sea Challengers, Los Osos, California, USA. 112 pp.
- BEHRENS, D.W. 1991. *Pacific Coast Nudibranchs, A Guide to the Opisthobranchs Alaska to Baja California*, 2<sup>nd</sup> ed. Sea Challengers, Monterey, California, USA. 107 pp.
- BEHRENS, D.W. 2004. Pacific Coast Nudibranchs — Supplement II: New species to the Pacific Coast and new information on the oldies. *Proceedings of the California Academy of Sciences* 55:11–54.
- BEHRENS, D.W., AND Á.VALDÉS. 2004. A new species of *Dendrodoris* (Mollusca: Nudibranchia: Dendrodorididae) from the Pacific Coast of North America. *Proceedings of the California Academy of Sciences* 55:408–413.
- BERTSCH, H. 1991. Seasonal, geographic and bathymetric distribution of opisthobranchs at Bahía de los Ángeles, Baja California, Mexico. *Western Society of Malacologists, Annual Report* 23:18.
- BERTSCH, H. 2000. Dr. Rudolf Stohler: Some personal remembrances. *The Veliger* 43(4):ii.
- BERTSCH, H., M.D. MILLER, AND A. GRANT. 1998. Notes on opisthobranch community structures at Bahía de los Ángeles, Baja California, Mexico. *Opisthobranch Newsletter* 24:35–36.
- BRODIE, G.D. 2001. Some comparative histological aspects of the dendrodorid genera *Doriopsilla* and *Dendrodoris* (Opisthobranchia: Nudibranchia). *Bollettino Malacologico, Roma* 37:99–104.
- BRODIE, G.D., AND G. CALADO. (In press.) *Dendrodoris arborescens* (Collingwood, 1881) (Mollusca: Nudibranchia): larval characteristics reveal a masked porostome. *Records of the Western Australian Museum*. Supplement. World Malacology Conference Opisthobranch Symposium.

- BRODIE, G.D., R.C. WILLAN, AND J.D. COLLINS. 1997. Taxonomy and occurrence of *Dendrodoris nigra* and *Dendrodoris fumata* (Nudibranchia: Dendrodorididae) in the Indo-West Pacific Region. *Journal of Molluscan Studies* 63:407–423.
- ELIOT, C.N.E. 1906. The genus *Doriopsilla* Bergh. *Journal of Conchology* 11:366–367.
- GRAY, J.E. 1847. A list of the genera of recent Mollusca, their synonyma and types. *Proceedings of the Zoological Society of London*, pt. 15:129–219.
- GODDARD, J.H.R. 2005a. Developmental mode in benthic opisthobranch molluscs from the northeast Pacific Ocean: feeding in a sea of plenty. *Canadian Journal of Zoology* 82:1954–1968.
- GODDARD, J.H.R. 2005b. Ametamorphic direct development in *Dendrodoris behrensi* (Nudibranchia: Dendrodorididae), with a review of developmental mode in the family. *Proceedings of the California Academy of Sciences*, ser. 4, 56:201–211.
- GOSLINER, T.M., M.C. SCHAEFER, AND S.V. MILLEN. 1999. A new species of *Doriopsilla* (Nudibranchia: Dendrodorididae) from the Pacific Coast of North America, including a comparison with *Doriopsilla albopunctata* (Cooper, 1863). *The Veliger* 42:201–210.
- LEE, R.S., AND P. BROPHY. 1969. Additional bathymetric and locality data for some opisthobranchs and an octopus from Santa Barbara County, California. *The Veliger* 12:220–221.
- MCDONALD, G. 1983. A Review of the “Nudibranchs of the California Coast.” *Malacologia* 24:114–276.
- MCDONALD, G., AND J. NYBAKKEN. 1981. *Guide to the Nudibranchs of California. Including most species found from Alaska to Oregon*. American Malacologists, Inc., Melbourne, Florida. 72 pp.
- PRUVOT-FOL, A. 1930. Du genre *Dendrodoris* Ehrenberg et de ses rapports avec le genre *Doriopsis* Pease et avec quelques autres. Note sur la taxonomie des nudibranchs. *Bulletin du Museum d'Histoire Naturelle*, Paris, ser. 2, 2(3):291–297.
- PRUVOT-FOL, A. 1954. *Mollusques Opisthobranches*. Faune de France, vol. 58. 460 pp.
- RUDMAN, W.B. 2003. *Dendrodoris* sp. 4. In: Sea Slug Forum. Australian Museum, Sydney, Australia. <<http://www.seaslugforum.net/factsheet.cfm?base=dendsp4>>.
- STEINBERG, J. 1961. Notes on the Opisthobranchs of the West Coast of North America. *The Veliger* 4:57–63.
- THOLLESSON, M. 2000. Increasing fidelity in parsimony analysis of dorid nudibranchs by differential weighing, or a tale of two genes. *Molecular Phylogenetics and Evolution* 16:161–172.
- VALDÉS, Á. 2002. A phylogenetic analysis and systematic revision of the cryptobranch dorids (Mollusca, Nudibranchia, Anthobranchia). *Zoological Journal of the Linnean Society* 136:535–636.
- VALDÉS, Á. 2003. Preliminary molecular phylogeny of the radula-less dorids (Gastropoda:Opisthobranchia) based on 16S mtDNA sequence data. *Journal of Molluscan Studies* 69:75–80.
- VALDÉS, Á., AND D.W. BEHRENS. 1998. A new species of *Doriopsilla* (Mollusca, Nudibranchia, Dendrodorididae) from the Pacific coast of North America. *Proceedings of the California Academy of Sciences*, ser. 4, 50:307–314.
- VALDÉS, Á., AND T.M. GOSLINER. 1999. Phylogeny of the radula-less dorids (Mollusca, Nudibranchia), with the description of a new genus and a new family. *Zoologica Scripta* 28:315–360.
- VALDÉS, Á., AND J. ORTEA. 1997. Review of the genus *Doriopsilla* Bergh, 1880 (Gastropoda, Nudibranchia) in the Atlantic Ocean. *The Veliger* 40:240–254.
- VALDÉS, Á., J. ORTEA, C. ÁVILA, AND M. BALLESTEROS. 1996. Review of the genus *Dendrodoris* Ehrenberg, 1831 (Gastropoda: Nudibranchia) in the Atlantic Ocean. *Journal of Molluscan Studies* 62:1–31.
- WÄGELE, H., G. BRODIE, AND A. KLUSSMANN-KOLB. 1999. Histological investigations on *Dendrodoris nigra* (Stimpson, 1855) (Gastropoda, Nudibranchia, Dendrodorididae). *Molluscan Research* 20:79–94.
- WOLLSCHIED-LENGELING, E., J. BOORE, W. BROWN, AND H. WÄGELE. 2001. The phylogeny of Nudibranchia (Opisthobranchia, Gastropoda, Mollusca) reconstructed by three molecular markers. *Organisms Diversity and Evolution* 1(4):241–256.